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## A science-based interpretation of ongoing productivity of commercial, recreational or Aboriginal fisheries

## Une interprétation scientifique de la productivité continue des pêches commerciales, récréatives ou autochtones

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#### Abstract

Canada's Fisheries Act, amended in 2012, refers to 'sustainability and ongoing productivity of commercial, recreational or Aboriginal fisheries'. A conceptual framework for a sciencebased interpretation of ongoing productivity of fisheries is described. The productivity of a fish population is determined by vital rates (reproduction, growth and survival) and by life history traits (fecundity, age at maturity). The vital rates regulate population abundance, biomass and fish production. Fish production rate is the rate that biomass is accumulated per unit area per unit of time. Fisheries yield (landings) is a function of total fish production. Fisheries are often comprised of more than one population or species. Fisheries productivity, in the context of the Fisheries Protection Provisions (FPP), is interpreted as the sustained yield of all component populations and species, and their habitat, which support and contribute to a fishery in a specified area. Sustainability, biodiversity, and measurement uncertainty are key dimensions of ongoing productivity that need to be kept in mind within the conceptual framework. Population abundance is dynamic over time, but to be sustainable, the management of habitat-related physical impacts and other threats must be done such that populations can rebuild within a reasonable period of time if they become temporarily depleted. The new Provisions focus on a larger, functional spatial scale (landscape, population or fishery) than the localized project scale that was the case historically. Three categories of projects that vary in spatial scale and complexity were identified: small scale projects involving loss of habitat area, diffuse projects that impact vital rates through changes in habitat quality, and large projects that result in ecosystem transformation. To be operational and to measure impacts at a landscape scale, the appropriate surrogates of productivity will vary depending on the project category, ranging from habitat-based approaches, where ongoing fish productivity is inferred from the quantity and quality of habitat, to more direct measures of fisheries productivity (such as yield) for larger scale projects. Two pressing needs for implementation are a clear description of the operational tools available to measure productivity at the landscape scale, and a new precautionary framework to guide fishery protection to maintain productivity and ecosystem function.


## RÉSUMÉ

La Loi sur les pêches fédérale, modifiée en 2012, fait référence « à la durabilité et à la productivité continue des pêches commerciales, récréatives et autochtones ». On décrit un cadre conceptuel pour une interprétation scientifique de la productivité continue des pêches. La productivité d'une population de poissons est déterminée par des indices vitaux (reproduction, croissance et survie) et des paramètres du cycle biologique (fécondité, âge à la maturité). Les indices vitaux régissent l'abondance de la population, la biomasse ainsi que la production de piscicole. Le taux de production du poisson est le taux correspondant à la biomasse accumulée par unité de surface par unité de temps. Le rendement de la pêche (débarquements) est fonction de la production piscicole totale. Les pêches ciblent souvent plus d'une population ou espèce. La productivité des pêches, dans le contexte des dispositions sur la protection des pêches, est interprétée comme étant le rendement soutenu de toutes les composantes des populations et des espèces, ainsi que de leur habitat, qui soutiennent la pêche dans une zone définie et qui y contribuent. La durabilité, la biodiversité et l'incertitude relative aux mesures sont les principaux éléments de la productivité continue qui doivent être pris en compte en ce qui a trait au cadre conceptuel. L'abondance de la population est dynamique à long terme, mais pour qu'elle soit durable, il faut gérer les impacts physiques sur l'habitat et les autres menaces de manière à ce que les populations puissent se restaurer dans un délai raisonnable en cas d'épuisement temporaire. Le nouveau programme de protection des pêches met l'accent sur une échelle spatiale plus générale et fonctionnelle (paysage, population ou pêche) que celle généralement utilisée par le passé. On a défini trois catégories de projets dont la complexité et l'échelle spatiale varient : des projets à petite échelle associés à une perte de la superficie d'habitat, des projets diffus qui ont une incidence sur les indices vitaux à cause de changements dans la qualité de l'habitat, et des projets à grande échelle qui entraînent une transformation de l'écosystème. Afin de pouvoir être opérationnels et mesurer les impacts à l'échelle du paysage, les substituts appropriés de la productivité varieront selon la catégorie du projet, allant d'approches fondées sur l'habitat, pour lesquelles la productivité continue du poisson est déduite à partir de la superficie et de la qualité de l'habitat, à des mesures plus directes sur la productivité des pêches (comme le rendement) pour des projets à plus grande échelle. Deux besoins urgents de mise en œuvre sont une description claire des outils opérationnels disponibles pour mesurer la productivité à l'échelle du paysage, et un nouveau cadre de précaution pour orienter la protection du poisson afin de maintenir la productivité et la fonction de l'écosystème.

## 1. ONGOING PRODUCTIVITY

The purpose statement of the Fisheries Protection Provisions in the 2012 revisions to the Fisheries Act (s 6.1) is 'to provide for the sustainability and ongoing productivity of commercial, recreational or Aboriginal fisheries'. The term 'ongoing productivity' is stated again in section 6 as the first of four factors that must be taken into account in making fisheries protection decisions. Section 6.1(a) is 'the contribution of the relevant fish to the ongoing productivity of commercial, recreational or Aboriginal fisheries'.

The objective of this paper is to provide an operational interpretation of 'ongoing productivity'. Many of the threats to fisheries that will be regulated by DFO are physical impacts, often habitat-related, that occur at the scale of individual works, activities or undertakings. The challenge is how to connect these physical impacts to the ongoing productivity of commercial, recreational and Aboriginal (CRA) fisheries. To make this connection, the first step is to move toward a functional interpretation of productivity, which not only has a sound science base, but also can be applied in a consistent manner under a range of operational circumstances in marine, coastal, estuarine, riverine or lacustrine areas.

## CONCEPTUAL INTERPRETATION

Ecological productivity is defined by Oxford Dictionaries Online as 'the rate of production of new biomass by an individual, population, or community' or 'the fertility or capacity of a given habitat or area' (e.g., 'nutrient-rich waters with high primary productivity'). To elaborate on an interpretation of ongoing productivity with respect to CRA fisheries, we start from a species and population context, and then move to a fisheries and ecosystem perspective. The ultimate goal is to provide an operational interpretation consistent with an ecosystem framework for fisheries protection. Much of the discussion below provides a conceptual framework for productivity that can be used in the real-world decision making, and helps to clarify the properties that indices and units must have to inform the operational application and measurement of ongoing productivity. We encourage the use of common terminology (Randall 2003) for Fisheries Protection and Ecosystem and Fisheries Management.

## Productivity

Productivity of a fish population is determined by the vital rates of reproduction, growth and survival, and life history characteristics of the population such as fecundity and age at maturity. Key vital rates are used as measures of productivity, and they are the factors that result in population abundance or biomass The United Nations Food and Agriculture Association (FAO), Fisheries Department, describes the factors that affect productivity of a stock: 'relates to the birth, growth and death rates of a stock. A highly productive stock is characterized by high birth, growth and mortality rates, and as a consequence, a high turnover and production to biomass ratios (P/B)' (www.fao.org/fi/glossary/default.asp); alphabetical list of terms). Productivity of a population is inherently reflective of a species' life history strategy, which often involves suites of co-evolved traits (e.g., age at maturity, longevity, fecundity, etc.) that ultimately dictate their productivity (Charnov 1993; Musick 1999). The three basic vital rates of reproduction, growth and survival are also affected by threats (stress), including declines in habitat suitability or fishing. Expected changes to these rates can be used to measure the potential effects of threats on productivity (Power 2007).

From a population-level perspective sustained exploitation by a fishery is predicated on the productivity of the population being sufficient to allow harvest. The intrinsic rate of population growth ( $\lambda=\mathrm{N}_{t+1} / \mathrm{N}_{\mathrm{t}}$ ) is a summary metric that is used to describe population productivity. When the population is increasing either as changes in abundance or biomass over time, $\lambda>1$. In standard fish population theory, populations have their highest rate of intrinsic growth when spawners are adequately numerous to saturate suitable habitat for eggs and early larvae, but overall abundance of each life history stage is low enough that competition for limiting resources (food, space) is low. When a population is near its carrying capacity, density-dependent processes strongly constrain further increases in abundance and no population increase is expected ( $\lambda \approx 1$ ). Populations with a higher productivity can be sustainably exploited at higher rates. Productivity varies within populations over time (Bradford and Irvine 2000; Peterman and Dorner 2012), or spatially among populations of the same species (MacKenzie et al. 2003; Mantzouni et al. 2010), because of changes differences in environmental factors (e.g., temperature, ocean currents) or interactions with other populations or species (competition, predation).

Recruitment (the production of new individuals for the adult population) often can serve as a measure of productivity. A key aspect of recruitment rate is the slope at the origin of stock recruitment (SR) relation. This is the maximum possible rate of production of new recruits per unit of adult spawner abundance or biomass, when density-dependent processes are at their weakest. Beverton-Holt and Ricker SR models with biological reference points are shown in Fig. 1. However, there are often statistical challenges with this approach, as many years of stock and recruit data are required for robust fits to S-R data. The SR relationships are not linear because density-dependent constraints increase with increasing abundance. The maximum rate of recruitment potential is measured as the expected number of recruits per spawner when the numbers of spawners is small (slope at the origin; e.g., Myers et al. 1997).

The ubiquity of density-dependent feedback processes in the juvenile stages is central to sustainable harvest levels, and consequently to decision-making about sustainable exploitation rates and patterns. Because direct measures of density-dependent feedback processes are hard to make, surrogates must incorporate this concept when the necessary data do not exist to parameterize an S-R functional relationship for a stock. In general, threats to the population that occur prior to the density-dependent stage will have less impact on population productivity than those that take place after density-dependent mortality occurs (Power 2007), because of the inherent compensation properties of densitydepending population regulation processes. A reduction in abundance in an early life stage will be compensated to some extent by lower mortality at the density-dependent stage. Only very strong density-dependent mortality can completely offset losses in the early life stages, particularly when such losses are anomalously high. Such situations are reported in some stream-dwelling salmonids that have very strong density dependence and can withstand large losses of spawners or eggs without significant effect on smolt production (Bradford et al. 2000). However, the density-dependent processes cannot compensate fully for impacts that reduce a habitat carrying capacity (whether the impacts are human or not) when that habitat is used by life history stages after the main density-dependent filter has been applied.

## Fish Production

The population vital rates, identified in the previous section, determine the fish production rate which in turn determines the potential yield to fisheries. Fish production rate is the 'total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time' (Ricker 1975). Fish production has a spatial and temporal
context, and the production of a fish population depends on the amount and quality of habitat required for each life stage. The unit of time for measurement of production is often one year, and the units of production are total numbers of fish or kilograms (produced) for a specific species and fishing area (number $\mathrm{yr}^{-1}$ or $\mathrm{kg} \mathrm{yr}^{-1}$ ), or as relative units of kilograms (or number) per hectare per year ( $\mathrm{kg} \mathrm{ha}^{-1} \mathrm{yr}^{-1}$ ).
There are many methods and models for estimating fish production. The instantaneous growth method (Chapman 1978), where $P$ is calculated as the product of growth $\left(G_{\Delta t}\right)$ and average biomass ( $B$ ) for a defined time period ( $\Delta t$ ), helps conceptualize production as the dynamics involving growth and survival of all cohorts up to and during the interval of interest, with recruitment rate determining the initial year-class size. Mertz and Myers (1998) provide simplified but more detailed formulae for production, where growth is offset by losses from natural morality (plus fishing mortality if the population is being harvested).

Production as a rate is rarely measured directly, but recognition of the concept of production is central to any operational framework that has a sound scientific basis. Our interpretation of practical and attainable measures of surrogates of production and their limitations are discussed in the Operational Implications section.

The ratio of mean annual production to mean annual biomass $(\mathrm{P} / \mathrm{B})$ is a measure of the turnover rate of a population, and is linked to production and productivity for both fishes and aquatic invertebrates (Dolbeth et al. 2012). The instantaneous growth rate equations (above) can be restructured to show that the $\mathrm{P} / \mathrm{B}$ ratio is equal to biomass-average somatic growth ( $\mathrm{P} / \mathrm{B}=\mathrm{G}_{\Delta t}$ ). $\mathrm{P} / \mathrm{B}$ has been shown empirically to be inversely related to body size and life span (Dickie 1972; Banse and Mosher 1980; Peters 1983). Randall and Minns (2000) used allometry with fish size to estimate $\mathrm{P} / \mathrm{B}$ and, subsequently to parameterize a production index based on the product of $P / B$ and seasonal average fish biomass. Average fish biomass and fish production rate, by calculation, are highly correlated. For the purpose of an operational interpretation of productivity, $\mathrm{P} / \mathrm{B}$ can be a shortcut method of estimating production rate, noting that ratio estimators have additional statistical problems.

## Yield

Yield is the fisheries catch; units are often kg or number per area per unit time. Fishing catch and yield are often used interchangeably; exceptions are if catch includes catch and release data, or if discarding of dead fish is common, in which cases catch statistics and yield (landings) would be different. Potential yield is a component of production, and for marine fisheries, production is frequently estimated from yield using suitable adjustment factors (Mertz and Myers 1998; Power 2007). Mertz and Myers (1998) indicated that yield could be used as a proxy for production if yield to production ratios were know. Recent research has shown there are many problems with using landings as an exact surrogate of stock biomass (Branch et al. 2011; Daan et al. 2011). For the data used by Mertz and Myers (1998), Y/P ratios were found to vary from 0.3 to 0.8 , depending on the species and trophic level.

The sustainable yield to a fishery is also proportional to the size of the population, which is often determined by a life stage that is limited by the amount of suitable habitat for it. Such limitations might be apparent by the size of the lake or stream, or more subtly, being defined by areas of suitable temperature, ocean currents, biological productivity or other factors. Bradford et al. (2000) describe examples of habitat limitation for Coho Salmon and Mantzouni et al. (2010) show relations between cod population size and habitat area.

Sustainable yield is often impacted by recruitment, the process that results in new individuals being added to the adult populations. Productive populations have higher rates
of juvenile production per spawner, usually because the environmental conditions and habitats available for spawning and rearing result in relatively good survival and growth and produce healthy recruits that can contribute to the adult population. Many populations are constrained by habitat limitation in the egg-to-juvenile stages (causing density-dependent mortality; Myers and Cadigan 1993; Bradford et al. 2000), and in these cases yield will be maximized by a combination of the amount and quality of habitat available at the pre-recruit or recruitment stages of a species' life history.

Sustainability is discussed further below in the context of ongoing productivity.

## Fisheries Productivity

Fisheries in a particular area are sometimes comprised of multiple populations or species. Ongoing productivity of CRA fisheries is interpreted here as the sustained yield of one or all CRA fish species that comprise a fishery in a specified fishing area. Ongoing is interpreted as being sustained productivity, as experienced by participants in the fishery at and just before the time of interest.

This text best describes our interpretation of 'sustainable and ongoing productivity of CRA fisheries' as stated in the new FPP. Supporting species (Kenchington et al. 2013) and the species and habitats that contribute to ongoing productivity (Koops et al. 2013) are implicitly included in this interpretation.

## Ecosystem Productivity

Ecosystem productivity is dependent on ecosystem structure and function (Worm and Duffy 2003; Naeem et al. 2012), and can be measured indirectly as multispecies cumulative biomass (for marine environments, see Bundy et al. 2012) or primary or secondary production (Dolbeth et al. 2012). The theory associated with ecosystem productivity is complex. Although it is conceptually important to include the concept of ecosystem productivity because of bottom-up influences on fisheries productivity, it is challenging to use this concept practically. Indices of factors influencing multi-species productivity at multiple trophic levels (e.g., total phosphorus, TP) are sometimes used as predictors in empirical whole-system models to estimate fish biomass or fisheries yield (Table 1). Ultimately, the fishable biomass cannot exceed a cap set by primary production (Pauly and Christensen 1995), but this upper bound is rarely reached because of other limiting factors. The effect of physical habitat modifications on ecosystem productivity will likely be manifested by its effect on the productivities of component species.

## PRODUCTIVITY AND SUSTAINABILITY

Sustainability is explicitly mentioned in s 6.1 of the Fisheries Act in the phrase "sustainability and ongoing productivity of commercial, recreational or Aboriginal fisheries".
The Webster's dictionary definition of sustainable is: 'of, related to, or being a method of harvesting or using a resource so that the resource is not depleted or permanently damaged'.
A commonly used definition of sustainable development is: "Development that meets the needs of the present without compromising the ability of future generations to meet their own needs." which is from the World Commission on Environment and Development's (the Brundtland Commission) report Our Common Future (World Commission on Environment and Development, 1987). The UNCED definition is the basis for Canada's government-wide Sustainable Development Policy.

The Federal Sustainability Development Act indicates that sustainability "means the capacity of a thing, action, activity, or process to be maintained indefinitely" (lawslois.justice.gc.ca). Sustainability is usually defined as achieving a balance between the carrying out of current-day activities while allowing for future generations to achieve their needs. Most definitions of sustainability recognize present day and future human needs for natural resources, and the limits of the natural environment to sustain growth. For fisheries, sustainability has been described at different scales by Hilborn (2005). The narrowest perspective concerns single populations or stocks and is often framed in the traditional fisheries management context of maintaining yield and historical allocations, both preferably within the relatively narrow bounds of an "optimal" value. Control systems attempt to regulate human activities (particularly fishing) in a manner to keep abundance and yield within acceptable levels (Rice 2009). Implicit in this approach is the notion of fundamental stability and resilience of the ecosystem (sometimes incorrectly characterized as the balance of nature') and that fish stocks can be sustained by adjusting harvest rates.

A slightly broader definition is based on the concept of intergenerational equity and aligns with the Bruntland Commission definition of sustainable development. This view recognizes that populations will fluctuate, and some may decline significantly with exploitation or changing environmental conditions, but the basis of fisheries (the target species and their ecosystem) should be managed such that future human needs can be satisfied. There is less focus, in this perspective, for maintaining current conditions, relative to the notion of maintaining conditions that will permit a fishery in uncertain, and likely different, future conditions. For example, Hilborn (2005) proposes that if a stock becomes depleted but can be rebuilt within a generation, then that could be considered a sustainable practice. Hilborn's broadest perspective considers a combined biological and human ecosystem and recognizes that a human system of exploitation can be sustainable despite large changes that can include changes to human societies and the ecosystems they use. This perspective is most consistent with modern day definition of sustainable development that is based on three axes: environmental protection, economic growth and social equity.

## Sustainability of fish populations

The sustainability and ongoing productivity of fish populations depends on the amount and quality of the habitats (Fig. 2) required for each life stage, interactions with other species, and the appropriate management of fisheries and anthropogenic threats. For long-term sustainability, it is important to acknowledge that known activities (e.g., fishing, physical impacts) can be managed, but unknown factors affecting productivity can only be reacted to, once detected.

Fish populations vary significantly at annual and longer time scales, and predictions of future states are highly uncertain. While the fluctuations of small pelagic fishes such as herring and sardines are well known, as population data accumulates for other species, it is apparent that large changes in abundance can occur, often independent of human factors such as habitat change or exploitation (Hilborn et al. 2003; Peterman and Dorner 2012). Thus sustainable fish populations are not constant ones, but rather are populations that have the inherent capacity to be productive when their habitats and environmental conditions permit.

## Sustainability and ongoing productivity of fisheries

Sustainable development is based on the premise that opportunities of future generations should not be compromised by present-day decisions or actions. For fisheries, this definition of sustainability allows for changes in individual populations or species, recognizing that individual components of a fishery (or an ecosystem that supports a fishery) will fluctuate
over time. The benchmark condition is not an unfished stock, rather it is a stock that is exploited but not to the point where future recruitment is diminished. Sustainability ensures that important or key species (Kenchington et al. 2012) are not driven by anthropogenic threats to levels of abundance that changes their role in the ecosystem, nor results in the impairment of the productivity or genetic potential of the species. Similarly, the structure and function of the supporting ecosystem are maintained to allow some combination of species or populations to be sufficiently productive to sustain a fishery. This view is supported by recent work on the notion of "biocomplexity" which argues that the productivity of individual populations constantly changes with environmental factors and we cannot predict which species or populations will flourish (or decline) in the future (Hilborn et al. 2003). Fisheries are most likely to be sustainable when both species diversity, and the genetic and population diversity within species is maintained (Hauser and Carvalho 2008). Analogies have been drawn between investment portfolio diversity and biocomplexity (Schindler et al. 2010) - in the financial world investors have poor success in picking stocks, and this has led to a strategy of managing risk and sustaining returns using a portfolio of diversified investments. Similarly, biologists have little success in anticipating changes in productivity in fish populations. Hilborn et al. (2003) proposed that the best strategy for sustainable fisheries is to ensure management decisions do not compromise the potential for any constituent population or species to contribute to future fisheries. A management strategy under this paradigm would include ensuring the potential productivity of the necessary habitats of all life stages for key populations and species within the portfolio. Other anthropogenic threats (pollution, non-endemic disease, invasive species, domestication/cultivation impacts) should be managed to allow for present day and future productivity. Lastly, the maintenance of intra-specific diversity should be achieved by protecting a sufficient number of population segments from extirpation through exploitation or other threats.

## Time and the sustainability and ongoing productivity of fisheries

The notion of allowing for present-day needs without compromising future conditions within the concept of sustainable development does not preclude short-term or transitory impacts on the environment. For example, rotational harvest strategies could cause local impacts but could be sustainable if the prospects for rebuilding were high under a reasonable time frame. Similarly, impacts to habitat caused by construction activities could also be managed in a manner that would not cause a long-term impact on productivity, although there could be short-term impacts to some cohorts until habitats recover.
There is no explicit guidance on the duration of impacts to fisheries productivity that would be consistent with the definitions for sustainability. The FAO's guidelines for deep-sea fisheries (FAO 2009) provide the following advice:
"Temporary impacts are those that are limited in duration and that allow the particular ecosystem to recover over an acceptable time frame. Such time frames should be decided on a case-by-case basis and should be in the order of 5-20 years, taking into account the specific features of the populations and ecosystems. In determining whether an impact is temporary, both the duration and the frequency at which an impact is repeated should be considered. If the interval between the expected disturbance of a habitat is shorter than the recovery time, the impact should be considered more than temporary. In circumstances of limited information, States and RFMO/As (regional fisheries management organizations and arrangements) should apply the precautionary approach in their determinations regarding the nature and duration of impacts."

An important point from the FAO definition is that reoccurring transitory threats could be considered permanent impacts if the habitats or stocks cannot recover between events. Examples could include rapid changes in flow in a regulated river, or repeated impacts to river or ocean floors such as dredging or bottom trawling.

For Pacific salmonids the concept of recovery in one generation (typically 4-6 years) after the cessation of the threat (in this case fishing; Johnston et al. 2000) was used to define abundance-based target reference points (Holt and Bradford 2011). This definition is roughly consistent with the FAO guidelines for recovery.

An example of a temporary threat that is limited in scope and duration is provided by studies on the impacts of pipeline crossings of streams (summarized by Lésveque and Dubé 2007). Typically, those activities result in the release of sediment and disturb the stream bed, which can cause short-term stress on fish and their food supply. However, recovery generally occurs within a year (or few years in some cases) after the scouring effects of the freshet. From a sustainable productivity perspective, the impact is shorter than the life cycle of stream-dwelling fish, and any impacts to productivity are expected to be short lived.

## PRODUCTIVITY AND BIODIVERSITY

The ecological concepts of ecosystem productivity, biodiversity and resilience are linked (Worm and Duffy 2003; Worm et al. 2006) and these linkages have received a great deal of attention in the scientific literature over the past 20 years (Naeem et al. 2012). The original purpose of this research was to investigate how biodiversity affected productivity via the simple question "does the production of biomass vary predictably with the change in species richness" (Naeen et al. 2012). While scientific debate continues on this subject, as richness is only one component of biodiversity (see Allen et al. 2002; Soininen et al. 2012; Naeen et al. 2012), a few generalities that are relevant to fisheries productivity have emerged.

A more diverse ecosystem tends to have higher overall productivity and is generally more resilient to perturbation, both natural and anthropogenic (Cardinale et al. 2006; Naeem et al. 2012; Worm et al. 2006), possibly because of the portfolio effect which was introduced earlier. Biological diversity is thought to stabilize ecosystem processes and the services they provide (Schindler et al. 2010). Biodiversity has several dimensions: taxonomic, phylogenetic, genetic, functional, spatial and landscape (Naeem et al. 2012). In fisheries, for example, landscape diversity and/or habitat complexity have been shown to positively correlate with both production (Carey et al. 2010) and yield (Bracken et al. 2007). Similarly, diversity in life history traits (a type of functional diversity) has been shown to increase productivity and resilience in relatively species poor salmonid communities (Hilborn et al. 2003; Gibson et al.1993).

A second trend that emerges from recent biodiversity research is that there are gradients of biodiversity that exist in nature within all the major ecosystem types (Allen et al. 2002; Oberdorff et al. 1995). Globally, biodiversity is highest in the tropics and reduces on a latitudinal gradient (Allen et al. 2002). This observation has been linked to both the availability of resources and temperature (Allen et al. 2002) although there is still debate on this topic (Soinien et al. 2012). On a regional or geographic scale physical factors such as ecosystem size (Oberdorff et al. 1995; Dodson et al. 2000; Dembkowski and Miranda 2012) and climate interact with historical factors such as dispersal patterns to determine species richness. Dispersal patterns have been shown to be particularly important for determining species composition and richness in Canada's freshwater fishes (e.g., Mandrak and Crossman 1992; Scott and Crossman 1964). Local biological, (i.e., predation and
competition) and physical factors (i.e., habitat complexity) which are nested in the two larger scales are then the final determinates of ecosystem biodiversity (Oberdorff et al. 1995).
Direct threats to biodiversity include over exploitation, pollution, habitat destruction/alteration and introduced species (Worm et al. 2006; Smith et al. 2012). Climate change may also indirectly affect biodiversity by changing habitat conditions (e.g., temperature regimes, flow patterns, ocean biogeochemistry etc.) and/or biological conditions especially with relation to introduced species (Smith et al. 2012). Management of the threats to biodiversity should strive to ensure healthy and productive aquatic ecosystems which in turn will produce healthy commercial, recreational and aboriginal fisheries. The fisheries protection provisions will focus on the threats to habitat and those posed by invasive species while other threats will be managed by different instruments and measures.

Projects that either remove a portion of habitat or reduce a habitat that appears to be plentiful are challenging to deal with from a biodiversity/productivity point of view. Habitat quality can have a large effect on population productivity (see elsewhere) as can single physical stressors (e.g. water temperature, sedimentation; Koops et al. 2013) but the question of how much habitat is required to protect biodiversity and ecosystem services such as fishery yield is a topic of much debate (Rolf 2009). Much of this debate is occurring in the conservation literature both for freshwater (Williams et al. 2011) and marine (Rolf 2009; Rondinini and Chiozza 2010) systems but the concepts and methods are relevant to habitat management practices. Rondinini and Chiozza (2010) recently reviewed quantitative methods for setting percentage area targets to protect habitat types for marine conservation and found that at present no one ideal method existed and the overall conservation goal and data availability really decided which method could be used. This means that these projects will still require management on a case by case basis using some form of risk assessment.
Introduced species or aquatic invasive species are another threat to biodiversity that will be managed by the fisheries protection provisions. Invasive species directly change species richness and through biological interactions can affect ecosystem functioning (Smith et al. 2012). Probably the best known example of this is the introduction of the zebra mussel to the Great Lakes which drastically changed water clarity in these systems (Strayer 2009). While the southern areas of Canada have had the most invasive species in the past and remain at risk to new invasions (Smith et al. 2012; Chu et al. 2003) range expansion related to climate change is also expected to affect the north (Prowse et al. 2009).
Ecosystems are complex and the changes induced by a habitat alteration/destruction or introduced species may not always be immediately evident, which makes predictions difficult. Couple this difficulty with fact that the results of diversity changes may take time to fully equilibrate (e.g., reservoir creation, see Milbrink et al. 2011) and the case for strong monitoring programs linked to an adaptive management framework can be made for projects that are expected to reduce ecosystem diversity, either through reduced habitat complexity or species richness. Finally it is important to point out that ecosystem changes that result in changes to local biodiversity can sometimes benefit preferred fisheries species. These situations, however, should be viewed as the exceptions rather than the expectations of biodiversity change.
Specifics of biodiversity components to support ongoing productivity of CRA fisheries are described in detail by Kenchington et al. (2013).

## 2. OPERATIONAL IMPLICATIONS

## SPATIAL SCALE

Consideration of spatial scale will play an important role in the assessment of a projectbased impact on fish or their habitat, and in the application of s. 6 in departmental decision making. The scale of a project's direct impacts are usually well defined, however, the spatial context in which those impacts are considered will affect the tools and metrics to be used and criteria (particularly the factors of section 6) to be used for decision making.

The 1986 Policy operated at the smallest spatial scale by attempting to mitigate or offset each habitat-based impact with the goal of maintaining or replacing the function of the impacted habitat. It was implicitly assumed this approach would minimize or negate the effects of the project at all broader spatial scales.

As indicated in Section 1 of this paper the revised Act seeks to "provide for the sustainability and ongoing productivity of CRA fisheries" suggesting that broader spatial scales than the project's immediate footprint are the most relevant scales for evaluation. Decisions about spatial scale are ultimately policy choices but there are some science-based issues that we consider here. We note that the discussion is focused on development projects, but could also apply to other non-project based threats to productivity (particularly Aquatic Invasive Species, AIS).

Scales larger than the project could be considered in at least three ways: landscapes, biological populations, or fisheries.

From a landscape-level perspective, the most likely scale that would be considered is matched to physical features that roughly support ecosystems. In freshwater these could be watersheds (likely mid-order), small and medium sized lakes, and basins or arms of larger lakes. In the coastal area individual estuaries or bays and physically defined areas of the ocean may be an appropriate scale for assessing projects. A landscape-based assessment might consider the amount and value of habitat of various types within the unit, the severity of existing impacts to the unit, and the project impact relative to these factors. Habitat-based assessment tools would predominate in this context, but habitat-based biological indicators (such as lower trophic levels) could also be used in cases where projects alter food or energy webs. The landscape-level approach is probably the scale that will be most appropriate for cumulative effects assessment, and is expected to be important for the definition of Ecologically Significant Areas, so there will be some commonalities if this scale is given prominence in evaluations.
A higher level of scale is biologically-based and considers the impacts of projects on CRA fishery species. A demographic or genetic definition of population could be used here. For restricted populations (those that occupy a lake or stream), the geographic scale of this approach may not differ from the landscape level one, but in other cases where populations are broadly distributed, the population scale could be much larger. A biologically-based definition of scale will likely entail a population-dynamics based approach to the assessment of project impacts, in order to evaluate the change to population abundance or productivity.
Finally, a potentially broad spatial scale is that of the fishery, depending on defining what constitutes a fishery. In some cases, the fishery is well-defined and the associated populations can be easily identified. In other cases the fishery has no clear boundaries and a decision about scoping will need to be made. These could include existing fishery management units, but could also include other factors based on local use, for example. An
assessment at this scale will ultimately attempt to estimate the changes to key fishery indicators (yield, catch rates, species composition, and others).

## THE PRECAUTIONARY APPROACH AND PRODUCTIVITY

Even in the most information-rich settings there will be uncertainty about the productivity of a population contributing to CRA fisheries, as well as the physical impact of an activity on the productivity, regardless of the spatial scale of the project. At the same time, the consequences of some impacts to a population's productivity could be serious and difficult to reverse. Under those circumstances, it is appropriate to apply precaution in decisionmaking (PCO 2003).

In fisheries harvest management, the application of precaution in decision-making is aided by a structured approach, using three categories of stock status (Healthy, Cautious, and Critical) and a rate of allowable impact (fishing mortality) that varies systematically with the category in which the stock falls, based on its assessment (Rice 2009). The framework is anchored by a limit reference point for stock biomass (the critical - cautious boundary), where fishing mortality is at the lowest level possible to achieve through management. This Limit Reference Point is in turn determined by a stock-recruit relationship or other appropriate method to estimate how stock productivity varies with stock size. The objective is to prevent the stock reaching a state (the Critical zone) where productivity is impaired such that stock rebuilding would not be rapid and secure if fishing mortality were minimized. The other key position on the stock status axis is the cautious / healthy boundary, whose position is determined by the overall uncertainty in the estimation of the Limit Reference Point, the estimation of annual stock size relative to that reference point, and the uncertainty about the effectiveness of management. That is, the higher the total uncertainty, the wider the Cautious zone. Thus when uncertainty is high management actions to reduce exploitation rate begin at larger relative stock sizes than when uncertainty is lower.

This framework is well grounded in theory and has proven to be operational over wide ranges of types of stocks and fisheries, and of quantities and qualities of data. Its performance is robust (guides management in the right direction and in the proper general magnitude of response) even if much more data and time-demanding approaches to supporting harvest decisions under uncertainty can be shown to be more precise for our most information-rich stocks.

The situation with implementing the new provisions of the Fisheries Act has some important similarities to harvest management as framed above. There will be uncertainty about how productivity of a population that is part of a CRA fishery varies with the state of the habitat, uncertainty about how an activity/undertaking will alter key characteristics of the habitat, and uncertainty about how effective any mitigation or compensation measures could be. In the major activities/undertakings to which the new provisions are intended to apply, there will be at least sometimes risk of harm that would be serious and difficult to reverse, especially since the alterations of habitat could be permanent. Therefore precaution will need to be applied in decision-making about these activities/undertakings, and a similar framework for guiding the advice on application of precaution will be needed.
Work has been done to generalize the fisheries precautionary framework to a much wider range of environmental issues, including habitat impacts (Rice 2009). The concepts all transfer fully to these broader contexts, but few operational applications have been attempted. However, any approach to implementing the new fishery protection provisions in specific cases is going to require at least general identifications of how productivity is expected to vary with habitat status, the point at which productivity has been impaired such
that improvement is no longer expected to be rapid and secure, and the uncertainty in these factors. Those are all the properties needed to adapt and apply the same three-category framework to fisheries protection as is done in fisheries management. There would be benefits to science, to management and policy, and for communications, if we are able to apply a known and tested framework in supporting the application of precaution implementing the fishery protection provisions of the Fisheries Act. These ideas will be fully developed by Koops et al. (2012), and are implicit in our discussion of operational implications above, and in the "applications" section below.

Uncertainty with respect to impacts to the affected habitat and species, and subsequently to the ongoing productivity of fisheries, would be directly related to the type of habitat and to the spatial scale of the project.

## APPLICATION

The application of the preceding ideas can be aided with a more explicit description of the types of projects that may be considered in decision-making. To simplify the discussion, we focus on development projects that would be handled by the referral process and define three categories of projects by their type of impact and scale as:

1. Smaller scale infills/alterations or exclusions (barriers) that render habitat unusable to fish populations ("destruction"). From a population/fisheries dynamics perspective these are less likely to affect the productivity of individuals of the impacted population; rather they may change the carrying capacity of the ecosystem. This will impact the size of the fish population and the sustainable yield (moving left along the horizontal axis of Figure 2) by removing habitat from the system. The magnitude of change to fisheries productivity will depend on the size of the project and the significance of the habitat being removed from the system.
2. "Diffuse" projects that affect productivity. These projects affect the quality of fish habitat and at least some could be considered a "permanent alteration". Vital rates of fish populations are impacted by the activity and this can cause productivity of individuals in the population to decrease. This is equivalent to moving downward along the vertical axis of Figure 2. Examples include flow alterations, non-lethal sediment discharges, nutrient inputs, temperature changes and riparian clearing that might be associated with a number of land-use activities. Projects involving noise, changes to ice regimes and large-scale substrate alterations from dredging, trawling, and those that cause mortality (entrainment in turbines, intakes) fit within this category as well. Aquatic invasive species can have similar impacts. The spatial scale of these projects can be highly variable but could be much larger than those of category 1.
3. Major projects that result in significant ecosystem transformation (e.g., hydropower resulting in river to reservoir transformation), or removal of the ecosystem from use (e.g., lake infills, other, large infills). These are dealt with by undertaking or requiring detailed case-specific studies and a variety of approaches can and are used to determine the existing productivity, and to make predictions about future conditions. Since these are whole ecosystem changes, incremental approaches would be of limited value. These assessments are usually managed by CEAA and the information requirements may differ from those required by the Fisheries Act.

These project categories are listed in order of increasing complexity of assessment, and likely in spatial scale. The categories, and the spatial scales identified in this section form a template that we use to provide some initial thoughts on ways to operationalize the concepts of "ongoing productivity of CRA fisheries" described in Section 1 of this report.

For smaller projects (mainly in the first category) it is unlikely that sufficiently sensitive metrics exist to measure the effects of the projects on fish production or fisheries productivity, particularly at the scales at which "fisheries" are typically defined, Habitatpopulation models could be used to link project impacts to productivity, but these would require data, assumptions, and making some difficult judgments about the spatial scale for the assessment (Minns et al. 2011).

For these projects, the objective of s.6.1 of the Act (provide for the sustainability and ongoing productivity of CRA fisheries) may be met by establishing that the habitats that are impacted are those of CRA species (or support species) and that the changes to the habitats will lead to negative impacts on fisheries productivity. As noted above and illustrated in Figure 2, destruction of habitat or other activities that reduce the habitat supply will ultimately impact fishery yield. Thus these projects can be adequately managed using habitat-based approaches (Table 1).

The second category of projects is likely to directly impact fish production and productivity. These can be assessed using the Pathways of Effects (PoE) approach (Jones et al. 1996; Clarke et al. 2008) which links changes in habitats to fish population vital rates and productivity. The PoE approach is qualitative, but likely can identify the direction of change in productivity, and determine if the change is meaningful in the context of the habitats affected. The scale of assessment is that of the project (but including downstream or vicinity effects).

A more detailed approach attempts to more directly measure impacts to productivity. However, production rate is not often directly measured because of the large data sets needed on seasonal growth and mortality (but see Rago 1984 for a production-based method of estimating the consequences (lost production) of fish entrainment at power plants). Rather, biological indices (e.g., fish biomass, salmonid smolt yield, fisheries landings, P/B, vital rates) or habitat surrogates such as habitat suitability indices or estimates of primary or secondary production can be used to indirectly evaluate projectrelated impact to fish production and productivity (Table 1 and Minns et al. 2011). This approach will require some consideration of the spatial scale of the assessment, either at the landscape or population scale.
Fish biomass or standing stock, averaged seasonally, is a common denominator for many of the above indices, as a proxy for production. Direct and indirect estimates of fish productivity as related to specific habitats, using biological indices (biomass, vital rates and others) or physical habitat surrogate methods, are summarized by Minns et al. (2011), along with a discussion of limitations and assumptions of the methods. Despite the need for further work, habitat surrogates can be used now as a practical option for measuring ongoing productivity (Bérubé et al. 2005; Minns et al. 2011). Nevertheless, it would be informative to review the efficacy of the various surrogates for application within the context of the new FPP.

Large projects are likely best evaluated by assessing changes in fish production and fisheries productivity. In some cases whole ecosystems will be lost and that impact can be expressed in terms of fish production or fishery-based statistics such as yield or use. In other cases the ecosystems can undergo large-scale transformations and the change to fisheries can be estimated using productivity or production measures. Bérubé et al. (2005)
and McCarthy et al. (2008) provide examples of habitat-based production models for evaluating large hydroelectric projects. Other approaches include habitat-related biomass, population structure and P/B to estimating production or yield (Randall and Minns 2000).

Changes to biodiversity resulting from larger-scale projects or impacts should also be considered but there is a paucity of scientifically established approaches currently available. As an example, the amount of impervious surface (IS; i.e., surfaces that prevent rainwater infiltration to soil such as pavement, buildings) within a watershed has been shown to be a good indicator of the effects of human development on stream biota (Uphoff et al. 2011, Wheeler et al. 2005). In general, ecosystems with IS values between 10 and 20\% have been shown to be biologically impaired (Uphoff et al. 2011; Wheeler et al. 2005) and this can lead to reductions in biodiversity and biomass (Stanfield and Kilgour 2006). In areas where species are at the limit of their geographic range a lower level of human disturbance corresponding to IS values in the 5\% range can create changes in biodiversity (Stranko et al. 2008). While it is important to note that most of this work has been conducted in freshwater systems a similar trend has been observed in estuaries (Uphoff et al. 2011). Further work of this type on linkages between biodiversity change, fisheries productivity and human activities is needed before more precise management advice can be provided.

Major projects need to consider the changes in biodiversity as there is potential for impacts that are not easily captured in fish production assessment and modelling. It is important to be mindful of the bidirectional nature of the biodiversity-productivity relationship (Worm and Duffy 2003). This means that any project that can be expected to reduce local species composition can be expected to reduce overall productivity and vice versa, any project that reduces overall productivity can be expected to reduce local biodiversity. At the same time, many types of changes to habitat features can reduce the quality of the habitat for one set of species but improve it for another set. Under the new FPP the relative importance of species as part of CRA fisheries may help to inform which of such "trade-offs" are of concern and which are acceptable. However, this is an area where there is little experience and little directed research, and there is a need for a focused effort at understanding the nature of the trade-offs that may be encountered as the FPP is implemented.
Projects that affect local biodiversity tend to change ecosystem structure and function either through major habitat alterations, fragmenting the ecosystem or cumulative impacts. A good example of such a large habitat change is the damming of rivers, either to produce electricity or provide water for irrigation (Clarke et al. 2008; Poff et al. 2007). These major projects can degrade the ecosystem by a number of pathways at once. Dams, for example, alter flows and create reservoirs which results in a change in community structure, productivity (Milbrink et al. 2011) and can potentially fragment the ecosystem (Nilsson et al. 2005). Currently there is a great deal of scientific interest in measuring connectivity in both freshwater (Cote et al. 2009, Bourne et al. 2011) and marine systems (Botsford et al. 2009) and some specific thresholds have been proposed (Perkin and Gido 2011). A more detailed review of this subject might provide guidance to managers.
In summary, we suggest that the implementation of the new measures of the Fisheries Act can be achieved with a pragmatic approach that takes advantage of existing habitat-based approaches for smaller projects, and the use of direct measures, proxies and surrogates for productivity for larger ones. For major projects productivity-based approaches that evaluate impacts to fisheries will be more meaningful than habitat measures when impacts to aquatic environments are evaluated in the environmental assessment process along with social, economic and other environmental effects.

## 3. IMPLEMENTATION IMPLICATIONS

The amendments to the Fisheries Act provide a focus to protect ongoing productivity to ensure sustainability of fisheries for commercial, recreational and Aboriginal use. This protection will be provided by managing threats such as the alteration or destruction of fish habitat and/or the introduction of alien species. These threats can have lasting effects on fish populations, ecosystem resilience and the sustainability of resource utilization. Therefore, knowledge of the linkages between habitat and population productivity will remain the overarching theme of science contributions in support of the implementation of the fisheries protection provisions.

Operationally, moving from a site level management approach to one that considers the ongoing productivity of populations and fisheries will require new operational tools. Scientific information will be important in the development of these tools and below is an initial list of tools that could be developed in the near to medium term (1-5 years). This list is not meant to be exhaustive; it can be added to and modified as consultation continues on the fisheries protection provisions.

- Guidance on the surrogate measures of productivity (i.e., Table 1). While this paper introduces some metrics, how and when to use each and their relationship to productivity could be the subject of a guidance document or training program for program staff.
- Improve and develop ecological spatial analysis tools. Link mapping of physical habitat (e.g., acoustic seabed mapping) to biological productivity both with respect to habitat utilization and quality.
- Provide guidance on the development of regional productivity benchmarks (e.g., Bradford et al. 1997; Cote et al. 2011).
- Continue to develop standards and thresholds for common project types that affect habitat (e.g., ecologically significant flows).
- Provide guidance on the extrapolation of data in data poor situations (Kenchington et al. 2013).
- Develop and validate methods and metrics for cumulative impact assessment.
- Provide criteria and frameworks for designating Ecologically Significant Areas (ESAs).


## 4. CLIENT SUMMARY

The concept of 'ongoing productivity' of commercial, recreational or aboriginal fisheries' refers to a biological process, the product of which is catch in numbers or weight of fish in a particular habitat area on a sustained basis. Habitat-related physical impacts that affect productivity will impact the vital rates that determine production; specifically reproduction, growth and survival. The field measurement and tracking of ongoing productivity at different habitat spatial scales will often involve, directly or by inference, impacts on vital rates. Feasible field surrogates of productivity can be biology-based (fish abundance, catch, indices of production) or habitat-based, depending on the habitat and scale.
Sustainability and biodiversity are important dimensions to include in a conceptual definition of ongoing productivity. Sustainability, in a broad sense, means that current actions designed to manage threats to fisheries should ensure that future human needs can be
satisfied. The ecological concept of sustainability recognizes that populations fluctuate over time, but threats should be managed such that if depleted, there is a reasonable expectation of recovery in a short period of time. Fisheries are often based on more than one population or species, and therefore biodiversity comes into play. Natural gradients in biodiversity exist both globally and within Canada, and provide a background context for managing threats. Some thresholds that relate habitat disruption to biodiversity and productivity are discernible (e.g., imperviousness of watersheds, minimum flow, and sedimentation). A framework for evaluating thresholds in the context of contributions to CRA fisheries is being developed (Koops et al. 2013).

With the new focus in Fisheries Protection on the ongoing productivity of fisheries, the precautionary approach to management will apply. A framework relevant to Fisheries Protection is being developed. Uncertainty of impacts to populations and fisheries is related to the spatial scale of the impact. Because of potential impacts to productivity, the numerous small scale projects will continue to be relevant, as well as the larger scale projects. Areabased management tools (integrated fisheries management plans, Ecologically Significant Areas, and cumulative effects assessment) will be useful in future and provide support for an ecosystem-based framework for Fisheries Protection.

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## 6. TABLES

Table 1. Example surrogate measures of productivity.

| Measure | Scale | Predictors | References |
| :---: | :---: | :---: | :---: |
| Production | Small | habitat quality | Clarke and Scruton 1999 |
| Yield | Large (lake) | lake area, morphometry, light, thermal habitat | Marshall 1996; Lester et al. 2004 |
| Biomass | Large (lake) | TP, area, location | Downing and Plante 1993; Cote et al. 2011 |
| Smolts\& parr | Large \& small(rivers) | landscape, latitude | Bradford et al. 1997; Gibson 2006 |
| Abundance (density, CPUE) | Small/large | Habitat quality | McCarthy et al. 2008 |
| Population structure (P/B, body size) | Multiple scales | Habitat quality, community structure | Randall and Minns 2000; Bérubé et al. 2005 |
| Vital Rates (growth, survival, recruitment) | Multiple scales | Habitat quality | see Minns et al. 2011 for examples |
| Habitat (HSI, PHABSIM) | Multiple scales | Habitat quality | see Minns et al. 2011 for examples |

Table 2. Descriptive summary of operational implications.

## Measures of productivity

- Maintaining fish production, the core biological process leading to fisheries yield, is the foundation of ongoing productivity. Production rate per se is rarely measured but surrogate measures of productivity are available for populations, fisheries and ecosystems.
- Fish catch, abundance, biomass, vital rates, habitat metrics or empirical relationships can be used to measure productivity, depending on the spatial scale and complexity of the project (examples in Table 1).
- A pragmatic approach would be to use existing habitat-based approaches for smaller projects, and to use proxies of productivity such as biomass or yield for larger projects.
- Ecosystem drivers of productivity, such as total phosphorus, thermal properties or secondary production, are sometimes used as predictors in empirical models of fish biomass or yield.
- Physical habitat modifications affecting ecosystem productivity will likely be manifested in the productivity of component species.
- Constraints, limitations and uncertainty associated with using each type of measure of productivity need to be taken into account, to inform implementation of the FPP.
- Guidelines for developing regional benchmarks of productivity can be developed.


## Sustainability and productivity

- Although sustainability has three dimensions, ecological, social, and economic, only the ecological context is considered in this report.
- Populations are dynamic. One criterion for sustainability is that if populations are depleted, they must be able to rebuild within a generation.
- Ensure that management decisions do not compromise the potential for any constituent species or population to contribute to future fisheries productivity.
- This must include the protection of necessary habitats of all key species and populations.
- Definitions of sustainability can be used to inform "permanent".


## Biodiversity and productivity

- Productivity, biodiversity and resilience are positively related.
- Biodiversity has several dimensions: taxonomic, phylogenetic, genetic, functional, spatial and landscape. Biodiversity and habitat/landscape diversity are related.
- Quantification of some thresholds relating habitat disruption to biodiversity and productivity is available (e.g., imperviousness, flow, sedimentation).


## Spatial considerations

- Spatial scale and complexity of projects will vary from small (e.g., localized infills) to large (ecosystem transformation), and methods for measuring productivity will vary accordingly.
- For FPP, relevant spatial scales for measuring impacts to productivity are landscape, population and fishery, with landscape scale being the likely focus as ecosystem function often operates at this scale.
- Ecological Significant Areas are a potentially important tool for protecting ongoing productivity, but guidance is needed on criteria and frameworks for identifying ESAs.
- Integrated fisheries management plans, already available or planned for many areas, will be valuable for identifying regional conservation objectives relevant to ongoing productivity.
- Ecological Significant Areas and regional fisheries management plans could provide the spatial framework for cumulative effects assessment of diffuse projects.
- For data-poor areas, extrapolation of data from other areas with similar biota and habitat attributes will be necessary.


## 7. FIGURES



Figure 1. Conceptual diagram of salmonid stock-recruitment relationships (Beverton-Holt and Ricker) showing how the intrinsic rate of growth, $\lambda$, varies with abundance relative to the carrying capacity.


Figure 2. Relation between maximum sustainable yield (MSY) and population parameters for a hypothetical salmon population using the Ricker stock-recruit function, $R=S e^{a(1-S b)}$. Productivity is indexed by the ratio of returning recruits $(R)$ to the parent spawners $(S)$ at low abundance ( $R / S=e^{a}$ ). Habitat capacity or size is the Ricker b parameter, the unfished equilibrium. Contours of annual yield (thousands of fish) illustrate how a sustainable fishery depends on both the quantity (via b) and quality (productivity, a) of the population and its habitats.

